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Differential relationships between habitat fragmentation and within-population genetic diversity of three forest-dwelling birds

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4   Abridged title: Habitat fragmentation and population genetic variation

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Abstract Habitat fragmentation is a major driver of environmental change affecting

wildlife populations across multiple levels of biological diversity. Much of the recent research in

landscape genetics has focused on quantifying the influence of fragmentation on genetic

variation among populations, but questions remain as to how habitat loss and configuration

influences within-population genetic diversity. Habitat loss and fragmentation might lead to

decreases in genetic diversity within populations, which might have implications for population

persistence over multiple generations. We used genetic data collected from populations of three

species occupying forested landscapes across a broad geographic region: Mountain Chickadee

(*Poecile gambeli*; 22 populations), White-breasted Nuthatch (*Sitta carolinensis*; 13 populations)

and Pygmy Nuthatch (*Sitta pygmaea*; 19 populations) to quantify patterns of haplotype and

nucleotide diversity across a range of forest fragmentation. We predicted that fragmentation

effects on genetic diversity would vary depending on dispersal capabilities and habitat specificity

of the species. Forest aggregation and the variability in forest patch area were the two strongest

landscape predictors of genetic diversity. We found higher haplotype diversity in populations of

P. gambeli and *S. carolinensis* inhabiting landscapes characterized by lower levels of forest

fragmentation. Conversely, *S. pygmaea* demonstrated the opposite pattern of higher genetic

diversity in fragmented landscapes. For two of the three species, we found support for the

prediction that highly fragmented landscapes sustain genetically less diverse populations. We

suggest, however, that future studies should focus on species of varying life-history traits

inhabiting independent landscapes to better understand how habitat fragmentation influences

within-population genetic diversity.

Key words: haplotype diversity, mitochondrial DNA, nucleotide diversity, Poecile

gambeli, Sitta carolinensis, Sitta pygmaea

46   INTRODUCTION

Ecologists often study how habitat composition and configuration influences the abundance and

48   occurrence of organisms (Turner et al. 2001, Fahrig 2003), but in recent years, the field of

landscape genetics has focused on how these landscape features influence genetic variation

50   (Anderson et al. 2010, Sork and Waits 2010, Storfer et al. 2010). Landscape genetics studies

have successfully incorporated the role of isolation and geographic distance in explaining genetic

52   variation among populations (e.g., Jenkins et al. 2010); however, there has been a persistent

interest in examining how habitat composition and configuration influences genetic diversity

54   within populations (Bruggeman et al. 2010, Sork and Waits 2010, Thomassen et al. 2010). This

interest has been driven, in part, by the concern that habitat fragmentation might lead to

56   decreases in genetic diversity within animal populations, which might have strong implications

for the persistence of populations over multiple generations (Frankham et al. 2010).

58   The process of habitat loss and fragmentation produces landscapes characterized by

isolated habitat patches of decreasing size and continuity and has important implications on

60   genetic diversity. Landscapes characterized by habitat loss and fragmentation are thought to

support smaller effective population sizes (Wilcove 1985, Debinski and Holt 2000, Chalfoun et

62   al. 2002), which neutral theory predicts will lead to decreased genetic diversity (Hartl and Clark

2007). Empirical evidence seems to support this prediction as birds with relatively larger

64   populations and broader distributions are genetically more diverse (Moller et al. 2008). For many

species, one of the mechanisms driving this pattern is that fragmentation causes decreased rates

66   of individual movement and dispersal among isolated habitat patches (Belisle et al. 2001),

leading to a subdivided and more variable population (Boulinier et al. 1998, Boulinier et al.

68   2001, Donovan and Flather 2002). In turn, random genetic drift and reduced gene flow leads to

an eventual decline of within-population genetic diversity as a result of declining and/or

70   disconnected populations (Templeton et al. 1990, Young et al. 1996, Keyghobadi 2007).

Comparative studies on the genetic impact of habitat fragmentation among populations

72   generally support the prediction of reduced genetic diversity in fragmented landscapes

(Keyghobadi 2007). Many of these studies, however, are plagued by analytical and

74   methodological limitations. First, studies of habitat fragmentation often confound habitat loss

with the process of habitat fragmentation per se (the spatial breaking apart of habitat independent

76   of habitat loss) (Fahrig 2003). A potential reason for this limitation results from a lack of

replication of independent landscapes by which to assess variability in habitat configuration

78   (McGarigal and Cushman 2002). Second, most comparative studies compare genetic structure

within a control and fragmented landscape in the same geographic region. As a result, it is

80   difficult to identify which aspects of fragmentation might be driving changes in genetic

responses and differentiate those from broader-scaled regional patterns (Johansson et al.

82   2005). Third, few studies focus on multiple species with varying life history characteristics. It is

likely that species of different characteristics of dispersal and habitat specificity could mediate

84   the genetic response to fragmentation at a landscape scale (Van Houtan et al. 2007, Bowie 2011,

Callens et al. 2011). Genetic diversity is a population characteristic that should be particularly

86   sensitive to the spatial distribution of habitat, and there is a need to evaluate the characteristics of

habitat loss and fragmentation that could lead to genetic variation among multiple species

88   inhabiting a continuum of fragmentation.

We quantified patterns of within-population genetic diversity for bird populations

90   exposed to a range of habitat fragmentation for three species of passerine birds found throughout

the western United States: Mountain Chickadee (*Poecile gambeli*), White-breasted Nuthatch

92 (*Sitta carolinensis*) and Pygmy Nuthatch (*Sitta pygmaea*). Previous molecular analyses have

suggested that some of the range-wide patterns of genetic structure and among-population

94 diversity in these three species can be explained by historical isolation and subsequent expansion

from glacial refugia in the Pleistocene. In *P. gambeli*, two clades are consistent with isolation in

96 two refugia during glacial advances (Spellman et al. 2007), and among western populations of *S.

carolinensis*, two of three clades decrease in nucleotide diversity with increasing latitude, a

98 pattern consistent with expansion from southern glacial refugia (Spellman and Klicka 2007). For

S. pygmaea, expansion from a single glacial refugium in southern coastal California may have

100 led to a positive correlation of nucleotide diversity with longitude (Spellman and Klicka 2006).

However, these studies primarily focused on phylogeographic patterns of genetic diversity

102 among populations as opposed to genetic characteristics within independent populations.

Our objective was to use existing genetic data to test the relationship between habitat

104 fragmentation and within-population genetic diversity for the above three forest-breeding bird

species across a range of fragmentation. We predicted that the relationship between

106 fragmentation and within-population genetic diversity, as measured by haplotype and nucleotide

diversity, would vary among species according to their dispersal capabilities and habitat

108 requirements. Specifically, we predicted that the genetic diversity of the *P. gambeli*, with its

intermediate dispersal distance (McCallum et al. 1999) and habitat specificity might not vary

110 with fragmentation. We predicted that genetic diversity would be higher for the *S. carolinensis* in

fragmented landscapes, because of their longer dispersal distances (Grubb and Pravosudov 2008)

112 and relatively diverse habitat associations. Finally, we predicted that genetic diversity would

decrease in fragmented landscapes for the *S. pygmaea*, with its relatively poor dispersal

114 capabilities (Kingery and Ghalambor 2001) and strict habitat associations, because it would be

less likely to disperse across a fragmented landscape (Van Houtan et al. 2007). Generalist species

116   that exhibit relatively greater rates of dispersal should be less susceptible to the impacts of

habitat fragmentation and its associated processes that erode local genetic diversity over time

118   (Mech and Hallet 2001, Vandergast et al. 2007, Bowie 2011).

120   METHODS

Study species and genetic sampling

122   The distribution of each of our study species, *P. gambeli, S. carolinensis*, and *S. pygmaea*,

matches the distribution of their preferred forest habitats, coniferous forests, pine-oak and long-

124   needle pine, respectively. *Poecile gambeli* generally prefers montane coniferous forests and areas

dominated by pine, spruce-fir (Picea-Abies), and piñon-juniper (Pinus-Juniperus) (McCallum et

126   al. 1999). They will occur in mixed coniferous-deciduous habitats, but show preferential use of

conifer stands in these settings (McCallum et al. 1999). *Poecile gambeli* generally does not

128   migrate, but most yearlings exhibit natal dispersal, although young dispersers sometimes move

only as far as adjacent family groups (McCallum et al. 1999). *Sitta carolinensis* is more closely

130   associated with mature deciduous woodland, but can also breed in mixed deciduous, coniferous

forest, and a variety of montane woodland habitats (Grubb and Pravosudov 2008). They exhibit

132   somewhat irruptive migration and disperse up to 10 km in their first year, and although little is

known about natal dispersal distances for *S. carolinensis* (Grubb and Pravosudov 2008), mean

134   natal dispersal distances were less than 10 km in both a Belgian population (Matthysen and

Schmidt 1987) and German population (Winkel 1989) of Eurasian nuthatches (*Sitta europaea*).

136   Finally, *S. pygmaea* is the most specific in terms of habitat requirements. *Sitta pygmaea*

demonstrates a strong and almost exclusive preference for long-needled pine forests and are co-

138   extensive with that of ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), and

similar species (Kingery and Ghalambor 2001). They are also the most sedentary of the three

140   study species, with no migration and very short natal dispersal distances (< 500 m; Kingery and

Ghalambor 2001). Recorded mean natal dispersal distance for *S. pygmaea* centers around 287 m

142   (range = 0-533 m; Norris 1958). Evidence from individual populations also suggests that each

species is most likely to occur in relatively intact forested areas when compared to fragmented

144   landscapes (Brawn and Balda 1988, McCallum et al. 1999, Villard et al. 1999). Because of their

wide distribution across western North America and reliance on forest habitats, these species

146   created a suitable system to examine the influence of habitat fragmentation on within-population

genetic diversity.

148 	For each species, we used available sequences of the mitochondrial gene NADH

dehydrogenase subunit 2 (ND2; 1041 bp) from previously published phylogeographic studies on

150   the three species (Spellman and Klicka 2006, 2007, Spellman et al. 2007). We used previously

generated ND2 sequences from 216 *P. gambeli* individuals (22 populations), 92 *S. carolinensis*

152   individuals (13 populations) and 132 *S. pygmaea* individuals (19 populations; Fig. 1; Table 1).

The location of sampling sites emphasized protected areas with limited anthropogenic

154   disturbance (e.g., National Forests, State Parks, and State Game Preserves).

156   *Genetic data analysis*

Using ARLEQUIN v3.11, we estimated two indices of within-population genetic diversity:

158   haplotype diversity and pairwise nucleotide diversity (Excoffier et al. 2005). Haplotype diversity

is the probability that two randomly chosen haplotypes are different in the sample, whereas

160   nucleotide diversity is the average pairwise nucleotide difference between two sequences in each

population. Nucleotide diversity is haplotype diversity at the nucleotide level; therefore, it

162   captures not only how many different haplotypes are in a population, but also how different those

haplotypes are from each other. Low haplotype and nucleotide diversity can indicate low

164   underlying effective population size (Avise 2000), the influence of recent expansions from

glacial refugia (Spellman and Klicka 2006) or cyclical range shifts (Jaarola et al. 1999). These

166   two indices capture different aspects of genetic variation, but they may be statistically correlated.

We performed separate analyses for each of the species including sequences from all available

168   individuals from each population (Table 1).

170   *Landscape analysis*

We defined landscapes as a 10 km buffer around each sampled population's centroid to represent

172   the spatial extent encountered by most dispersing individuals within a single generation.

Although natal dispersal distances have not been fully characterized for our focal species,

174   available evidence suggests that these maximum dispersal distances are within a 10 km-radius

landscape (see *Study species and genetic sampling*).

176   We analyzed the 2001 National Land Cover Data (NLCD) to characterize the cover and

configuration of forest cover in the 10 km-radius landscape. The 2001 NLCD consists of 16 land

178   cover classes modeled over the conterminous United States at a 30 m cell resolution and a 0.40

ha minimum mapping unit (Homer et al. 2007). We calculated the proportion of each land cover

180   type within each landscape, but because the landscapes tended to be dominated by two primary

cover types (deciduous or coniferous forest and early-successional cover types), we chose to

182   aggregate the land cover classes to represent a binary habitat cover map of forest (including

deciduous/mixed forest or evergreen forest types) and non-forest (including early-successional)

184   cover types. Although there are many metrics available for quantifying landscape heterogeneity

(Cushman et al. 2008), we quantified fragmentation using a subset of metrics that have been

186   shown to characterize aspects of forest fragmentation important for forest-breeding birds (e.g.,

forest patch size variability and forest aggregation) (Table 2). The initial set of metrics used to

188   describe forest fragmentation included the percentage of landscape classified as forest (Forest),

area-weighted mean forest patch area (AREA_AM), forest patch area coefficient of variation

190   (AREA_CV), mean nearest neighbor distance (ENN), nearest neighbor distance coefficient of

variation (ENN_CV), area-weighted mean edge contrast (ECON), similarity index (SIMI), and

192   clumpiness index (CLUMPY) (McGarigal et al. 2002). Multicollinearity is a common problem

when using fragmentation metrics as predictors, and for each species we examined scatter plots

194   to identify the least correlated ($r < 0.5$) set of predictor variables. We included the proportion of

forest cover at a 100 km radius landscape (FOR) as a measure of regional habitat availability and

196   to account for processes that might be occurring over broader spatial scales and maximum

dispersal events (Tittler et al. 2009). We calculated all landscape metrics in FRAGSTATS

198   (McGarigal et al. 2002).

200   *Statistical analysis*

For each species, we used a generalized linear model with a Gaussian error distribution (GLM)

202   (Faraway 2006) and AIC_c-based model selection (Burnham and Anderson 2002) to identify the

most parsimonious model of the relationship between within-population genetic diversity and

204   forest fragmentation. Forest cover (at the 10 km landscape-scale), and regional forest availability

(at the 100 km landscape-scale) was included in every model to statistically examine the

206   variation in forest configuration while controlling for forest composition. All fragmentation

metrics were standardized for analysis. As the number of individuals sampled in a population can

208   potentially influence genetic measures (Landguth et al. 2010), we ran two-sided Grubb's tests for

each species to test for the presence of outliers in the number of sampled individuals (Grubbs

210   1950). A Grubb's test detects one outlier at a time, and the outliers are expunged from the

dataset and the test is iterated until no outliers are detected. Following the identification and

212   elimination of outliers, sample size (n) was included as a covariate in model selection. For all

model runs, we included a model that included only forest cover (at both landscape and regional

214   scales). We calculated the number of model parameters (K), AIC_c values, ΔAIC_c, and Akaike

weights (w_i). Models with a $\Delta AIC_c < 2$ were considered equivalent (Burnham and Anderson

216   2002). We calculated Nagelkerke R^2 for assessing the explained variation of the global model in

a likelihood framework (Nagelkerke 1991). We performed model selection using R (Version

218   2.10.1; R Development Core Team 2009) with the extension package MuMIn (Barton 2010).

220   *Spatial analysis*

We checked for spatial autocorrelation to quantify whether patterns in within-population genetic

222   diversity were associated with broader latitudinal gradients fragmentation (Spellman and Klicka

2006, 2007, Spellman et al. 2007) after accounting for the variation explained by forest cover

224   and fragmentation. We calculated spatial correlograms (Moran's *I*) on residuals of the model

with strongest support through model selection (Model 1 for each species) at different lag

226   distances (maximum lag distance = 200 km) and tested whether spatial autocorrelation was

significant through resampling with 10,000 iterations (alpha < 0.05) (Dormann et al. 2007). We

228   performed all spatial analyses using the R extension package ncdf (Dormann et al. 2007).

230   RESULTS

Genetic diversity within populations

232   We found within-population genetic diversity to be variable among populations (within-species)

both for haplotype diversity (*P. gambeli*: mean = 0.62 ± 0.26; *S. carolinensis*: mean = 0.77 ±

234   0.24; *S. pygmaea*: mean = 0.67 ± 0.23) and for pairwise nucleotide diversity (*P. gambeli*: mean =

0.0019 ± 0.0015; *S. carolinensis*: mean = 0.0021 ± 0.0015; *S. pygmaea*: mean = 0.0021 ±

236   0.0010). As expected, haplotype diversity was correlated with nucleotide diversity for all three

species (*P. gambeli*: r^2 = 0.41, *P* < 0.001; *S. carolinensis*: r^2 = 0.22, *P* = 0.04; *S. pygmaea*: r^2 =

238   0.63, *P* < 0.001).

240   *Patterns of forest fragmentation*

We found that the local 10 km landscapes surrounding the sampling locations consisted of two

242   primary land cover types, forested upland (characterized by natural or semi-natural wood

vegetation greater than 6 m tall) and shrubland habitats (characterized by natural or semi-natural

244   wood vegetation with aerial stems less than 6 m tall), and supported the analysis of these sites as

binary (forest vs. non-forest) landscapes. Shrubland (non-forest habitats) is a classification

246   representing natural vegetation (non-agricultural) as areas dominated by shrubs less than 5 m tall,

and is often also associated with grasses, sedges, herbs, and non-vascular vegetation.

248   For *P. gambeli* populations we found forest composition (10 km radius) ranging from

25% to 95% (mean = 62%) and regional forest composition (100 km) ranging from 0% to 70%

250   (mean = 21%). We found similar patterns for the landscapes surrounding *S. carolinensis*

populations, we found that forest composition ranged from 23% to 87% (mean = 61%) and

252   regional forest composition ranged from 1% to 50% (mean = 21%). *Sitta pygmaea* landscapes

were also characterized by a combination of forest and shrubland cover types with forest

254   composition ranging from 2% to 96% (mean = 50%) and regional forest composition from 0% to

65% (mean = 14%).

256

Genetic diversity and forest fragmentation

258   Normal-probability plots and histograms showed that normality for regression-model residuals

was met. For *P. gambeli*, sample size ranged from 4-19 individuals and the outlier test was

260   significant (U = 0.40, *P* = 0.003). As such, we iteratively removed populations with fewer than 5

and greater than 14 individuals sampled. Re-running the outlier test demonstrated that no more

262   outliers were detected. The uncorrelated set of metrics included AREA_CV and CLUMPY that

resulted in eight separate models. For haplotype diversity, we found that two out of four models

264   had support (ΔAIC_c < 2; Table 3). The model with the strongest support (w_i = 0.46) included the

forest cover only model, while the second best model (w_i = 0.18) included only CLUMPY. For

266   *P. gambeli*, haplotype diversity was slightly lower in landscapes with higher forest cover at

landscape (Forest; $\beta = -0.13 \pm 0.22$) and regional scales (FOR; $\beta = -0.03 \pm 0.23$), but these

268   relationships were highly variable. When forest aggregation (CLUMPY) was included in the

model (Model 1; Table 3), we found that haplotype diversity for *P. gambeli* was higher in

270   landscapes with a higher degree of forest aggregation (CLUMPY; $\beta = 0.06 \pm 0.05$; Fig. 2A). The

Nagelkerke R^2 for the global model was 0.41. For nucleotide diversity, we found that one model

272   had the strongest support (w_i = 0.60). Similar to haplotype diversity, we found that nucleotide

diversity was higher in landscapes of higher forest aggregation (CLUMPY; $\beta = 0.79 \times 10^{-3} \pm$

274   0.29×10^{-3}; Fig. 2B).

For *S. carolinensis*, sample size ranged from 5-11 individuals, no outliers were detected

276   (U = 0.70, *P* = 1), and the least correlated set of fragmentation metrics for *S. carolinensis* were

AREA_CV, SIMI, and CLUMPY. Combinations of these variables resulted in eight separate

278   models. For haplotype diversity, we found that two models had the highest support in model

selection (w_i = 0.86). The top model (w_i = 0.57) only included forest patch size variability as a

280   fragmentation metric (AREA_CV; Table 3). We found that *S. carolinensis* populations

inhabiting more fragmented landscapes with a higher variability of forest patch sizes (high

282   AREA_CV) had lower haplotype diversity ($\beta = -0.12 \pm 0.03$; Fig. 3). Haplotype diversity was

also slightly higher in more forested landscapes at regional scales ($\beta = 0.09 \pm 0.23$), although this

284   was highly variable. The second most supported model (w_i = 0.29), included sample size (*n*) and

showed a slightly positive relationship with haplotype diversity ($\beta = 0.03 \pm 0.01$). The

286   Nagelkerke R^2 for the global model was 0.78. When analyzing nucleotide diversity the model

including only forest cover had the most support (w_i = 0.78; Table 3) suggesting that none of the

288   fragmentation metrics provided sufficient explanatory power in describing the variation in

nucleotide diversity for *S. carolinensis*. In these models, nucleotide diversity was higher in more

290   forested landscapes at a local scale, but slightly lower in forested regions.

Sitta pygmaea populations ranged from 4-11 individuals sampled and the outlier test was

292   not significant (U = 0.82, *P* = 1). We included three uncorrelated fragmentation metrics

including AREA_CV, ENN_CV, and CLUMPY in model selection. Three out of six models had

294   support (Δ AIC$_c$ < 2), and the final model set included the model with forest cover only (Table

3). In contrast to *P. gambeli* and *S. carolinensis*, we found that the haplotype diversity of *S.*

296   *pygmaea* populations generally increased in more fragmented landscapes (Nagelkerke R^2 =

0.47). Haplotype diversity was lower in landscapes with higher forest aggregation (CLUMPY; *β*

298    $= -0.09 \pm 0.04$; Fig. 4) and higher in landscapes with more forest patch size variability

(AREA_CV; $\beta = 0.10 \pm 0.04$). Nucleotide diversity showed the same general patterns including

300   the forest cover only with highest support, given the data ($w_i = 0.44$), and lower nucleotide

diversity in landscape characterized by higher forest aggregation (CLUMPY; $\beta = -0.31 \times 10^{-2} \pm$

302   0.02×10^{-2}).

304   *Spatial autocorrelation*

We did not find any evidence of systematic patterns of spatial autocorrelation in the model

306   residuals for any species (Fig. 5). After inspecting the spatial correlograms, we concluded that

once the models incorporated the effects of forest configuration and composition, there were no

308   broader spatial patterns in unexplained variation of within-population genetic diversity

associated with geographic proximity.

310

DISCUSSION

312   We used existing genetic data on three forest breeding bird species to examine the relationship

between within-population genetic diversity and forest fragmentation across multiple

314   independent landscapes. We predicted that patterns of within-population genetic diversity with

fragmentation would vary among species as a consequence of differences in their degree of

316   habitat specialization or dispersal abilities. However, these patterns did not vary with life history

traits in the directions that we predicted. Specifically, we predicted that within-population

318   genetic diversity would be more likely to decline in response to habitat fragmentation among

habitat specialists and among weak dispersers (Bailey et al. 2007) because they would be less

320   likely to disperse through the intervening matrix between appropriate habitat fragments (and,

therefore, would be more genetically isolated) than species with relatively broad habitat

322   associations and stronger dispersal abilities. For two of the three species (*P. gambeli* and *S.*

carolinensis), we found evidence that higher within-population genetic diversity was associated

324   with landscapes characterized by lower levels of forest fragmentation. We found forest

aggregation (CLUMPY) and the variability in forest patch area (AREA_CV) to be the two

326   strongest landscape predictors of genetic diversity in these two species. These metrics captured

the characteristics of habitat fragmentation, where large, compact clusters of forest with low

328   variability in size supported populations with higher levels of within-population genetic

diversity.

330   Our findings for *P. gambeli* and *S. carolinensis* are consistent with the predominant

conclusion of a survey of studies comparing within-population genetic diversity between

332   fragmented and control landscapes: in 26 of 45 comparisons (~58%), studies found reduced

genetic differentiation associated with fragmentation (Keyghobadi 2007). However, nearly half

334   of these studies (*n* = 19) found no effect or even an effect in the opposite direction (Keyghobadi

2007). Likewise, in this study, we found patterns of higher within-population genetic diversity of

336   *S. pygmaea* in fragmented landscapes. In our study, genetic diversity was higher in fragmented

landscapes for the species that was the most specialized (Kingery and Ghalambor 2001,

338   Spellman and Klicka 2006) and the most sedentary (Kingery and Ghalambor 2001), *S. pygmaea*.

In contrast, *P. gambeli* and *S. carolinensis* have arguably broader habitat associations and

340   stronger dispersal abilities than *S. pygmaea* (McCallum et al. 1999, Grubb and Pravosudov

2008), yet both showed a reduction of genetic diversity with fragmentation. Information about

342   dispersal distances for these species (and for songbirds in general) is limited, and is likely to be

greater than the distances reported in the literature (Tittler et al. 2009). Nevertheless, the patterns

344 that we observed did not match our predictions based on their putative dispersal distances

relative to one another, or with their relative specificity of habitat associations.

346   The elevated genetic diversity of *S. pygmaea* in fragmented landscapes is further

surprising because of their cooperatively breeding social system. Many breeding pairs have one

348 or more male helpers, usually offspring from pervious broods (Kingery and Ghalambor 2001).

Some juveniles merge with neighbors from the previous winter's group (Guntert et al. 1988,

350 Sydeman et al. 1988). The short dispersal distances, natal philopatry, and habitat specificity of *S.*

pygmaea are typical of many cooperatively breeding species (Woxvold et al. 2006, Haas et al.

352 2010). Such characteristics likely contribute to geographic isolation and genetic structuring

among populations, and could increase the vulnerability of cooperative breeders to habitat loss

354 and fragmentation (Koenig et al. 1996, Walters et al. 2004, Haas et al. 2010). However,

cooperative breeders could be buffered from loss of genetic diversity in large fragments, from

356 which juveniles might not have to disperse to find a breeding vacancy (Walters et al. 2004).

More research is needed regarding how cooperative breeding could influence the relationship

358 between fragmentation and genetic diversity.

Studying the relationship between habitat and within-population genetic diversity using

360 contemporary landscape data can be problematic because variation quantified by molecular

markers such as mitochondrial DNA may reflect historic, rather than contemporary, patterns of

362 environmental variation (Frankham et al. 2010, Landguth et al. 2010, Sork and Waits 2010). As

an example, *S. pygmaea* exhibited a positive correlation between genetic diversity and increased

364 fragmentation and is the only species in the study with a single glacial refuge but a similarly

large contemporary distribution (Spellman and Klicka 2006). By contrast, *P. gambeli* and *S.*

366 *carolinensis* had lower diversity in fragmented landscapes and are phylogeographically

structured into two or more reciprocally monophyletic clades and expanded to occupy their

368 current distribution from two (or more) glacial refugia (Spellman and Klicka 2007, Spellman et

al. 2007). Given the difference of range expansion from a single versus multiple glacial refugia,

370 it is possible that the overall effective population size of *S. pygmaea* following expansion was

larger and the contemporary distribution was achieved later than in *P. gambeli* or *S. carolinensis*.

372 If this were true, then we would expect *S. pygmaea* to enter genetic drift equilibrium slower than

other species with smaller, more disjunct postglacial population size. Thus, *S. pygmaea* may not

374 have yet achieved this equilibrium, even though they have the lowest dispersal rates of the three

examined species.

376 In some studies, when both historic and contemporary land use data have been studied,

information about historic landscapes has proven to be a better predictor of current genetic

378 variation than contemporary habitat fragmentation (Keyghobadi et al. 2005a, 2005b, Holzhauer

et al. 2006). Mitochondrial markers generally reflect the genetic imprint of historical processes

380 occurring hundreds of years before present (Frankham et al. 2010), but the samples used in this

study were collected from natural areas less affected by modern day anthropogenic disturbance.

382 Hence, it is likely that the contemporary patterns and variability of fragmentation across the

study landscapes were sustained primarily by biophysical processes (e.g. soil type, topography,

384 moisture gradients) rather than caused by human activity (e.g., human development). That being

said, additional studies utilizing molecular markers (e.g., microsatellites) that may more readily

386 capture contemporary genetic patterns could provide further insight into the relationships

between patterns of landscape fragmentation and within-population genetic diversity we found.

388 Habitat fragmentation is a major driver of environmental change affecting avian

populations across multiple levels of diversity (Fahrig 2003). In recent years, landscape genetics

390 has focused on quantifying the effects of fragmentation and landscape connectivity on the

genetic structure among populations (Luque et al. 2012), but studies must continue to take a

392 landscape-scaled approach of quantifying how characteristics of habitat configuration are

correlated with within-population genetic variation among a wide range of landscapes. Using

394 genetic data from multiple populations across a broad geographic area, we found within-

population genetic diversity was generally higher in landscapes characterized by less fragmented

396 forest habitat for two out of three forest breeding birds. These findings support the prediction that

fragmented landscapes sustain genetically less diverse populations; however, we found the

398 opposite pattern for the species that would normally be considered most susceptible to

fragmentation effects due to its limited dispersal abilities and habitat specificity. For broader

400 generalization based on empirical data, studies on genetic diversity and multiple species of

varying life-history traits inhabiting multiple landscapes are needed.

402

406

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566   Figure Legends

FIGURE 1. Geographic locations of sampling points for *Poecile gambeli* (A.), *Sitta carolinensis*

568   (B.), and *Sitta pygmaea* (C.) in western USA. Labels represent population identifiers (see Table
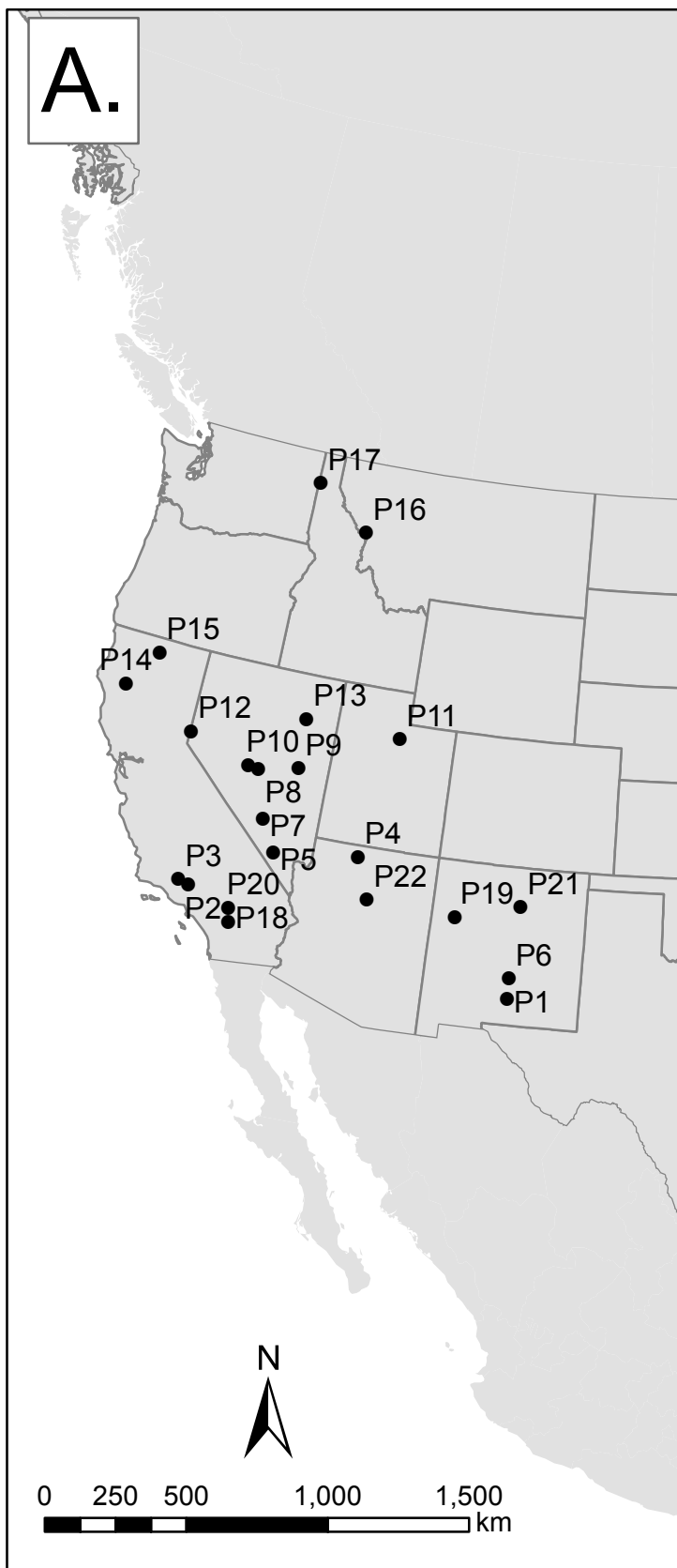
1).

570

FIGURE 2. For *P. gambeli*, haplotype diversity (A.) and nucleotide diversity (B.) was higher in

572   landscapes characterized by a higher degree of forest aggregation (CLUMPY).

574   FIGURE 3. For *S. carolinensis* populations, haplotype diversity was lower in more fragmented

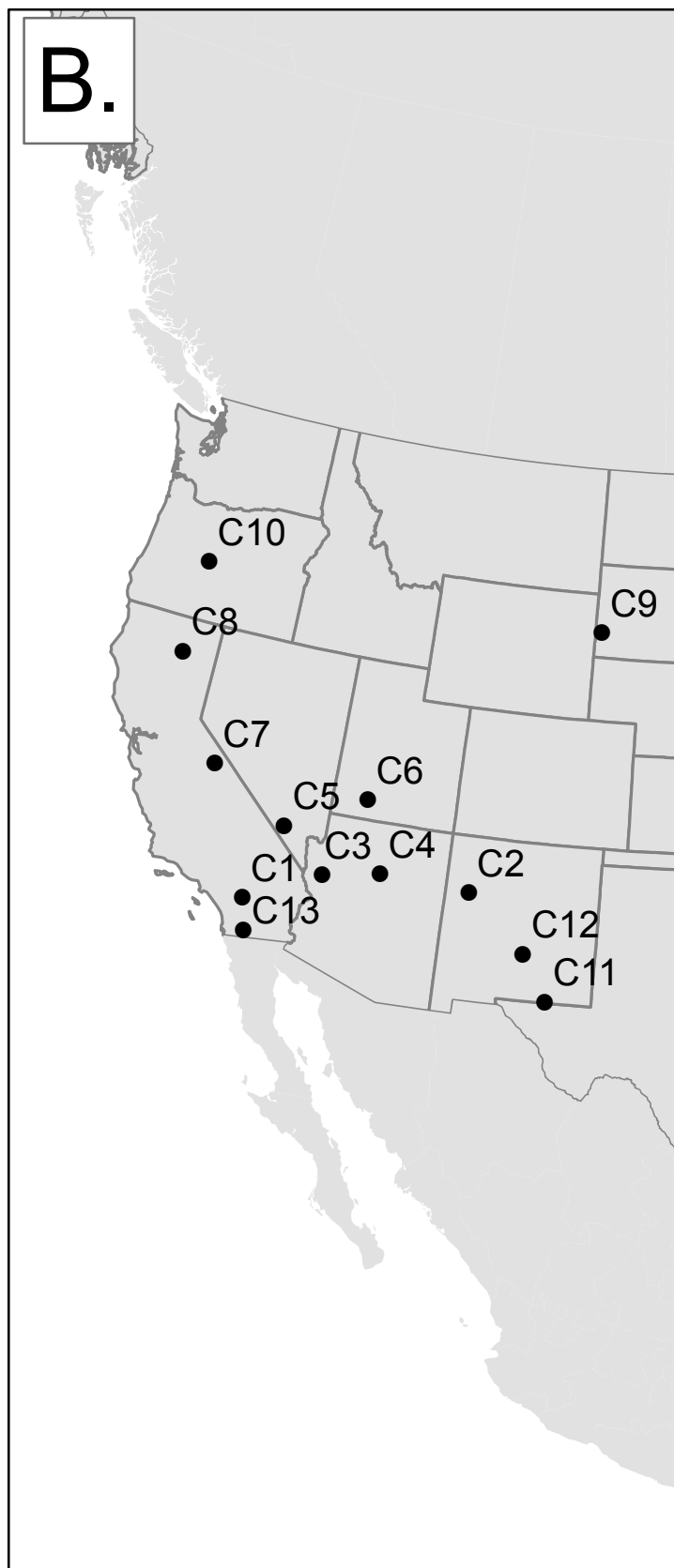landscapes characterized by higher variation in forest patch size (AREA_CV).

576

FIGURE 4. For *S. pygmaea*, haplotype diversity was lower in landscapes characterized by a

578   higher degree of forest aggregation (CLUMPY).

580   FIGURE 5. Spatial correlograms of GLM model residuals for *P. gambeli* (circles), *S.*

carolinensis (squares) and *S. pygmaea* (triangles) for haplotype (A.) and nucleotide (B.)

582   diversity. Filled symbols indicate significant spatial autocorrelation ($P < 0.05$) based on 10,000
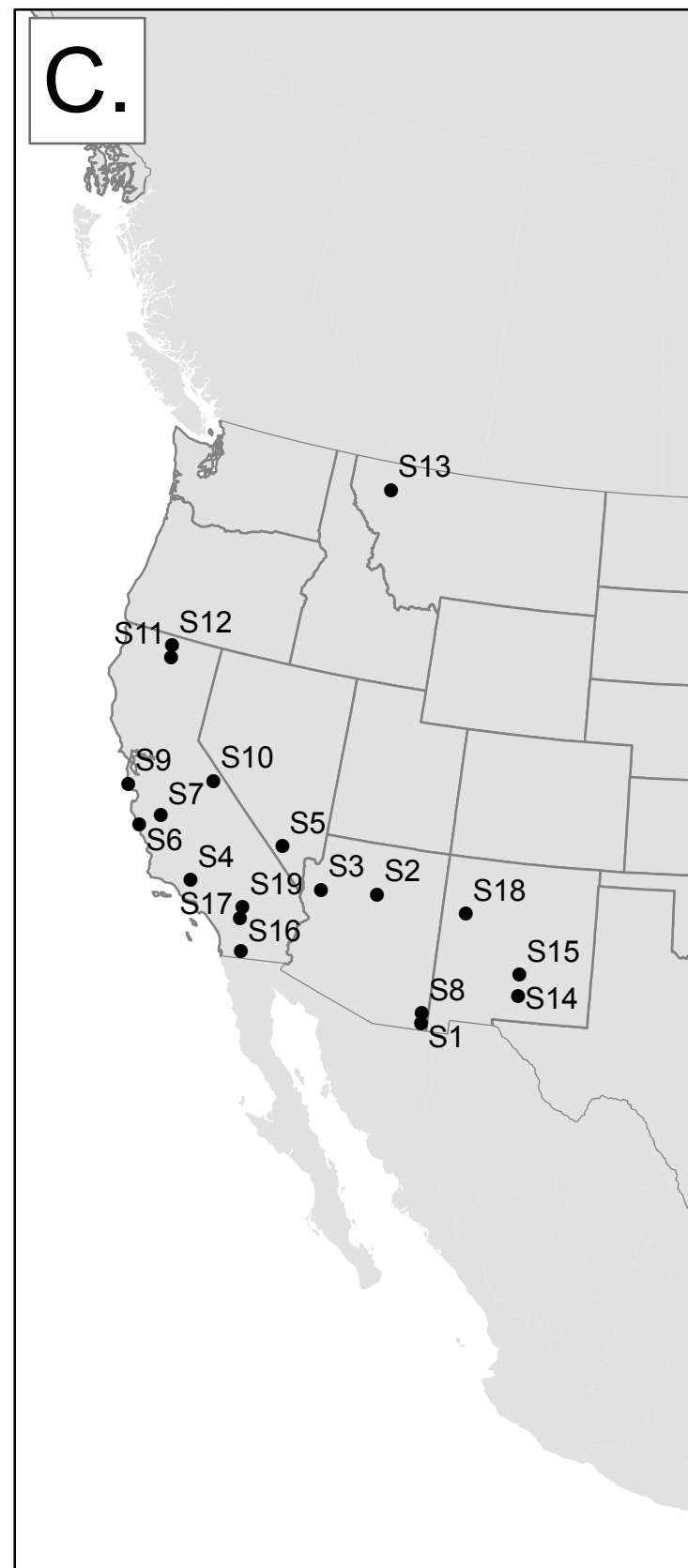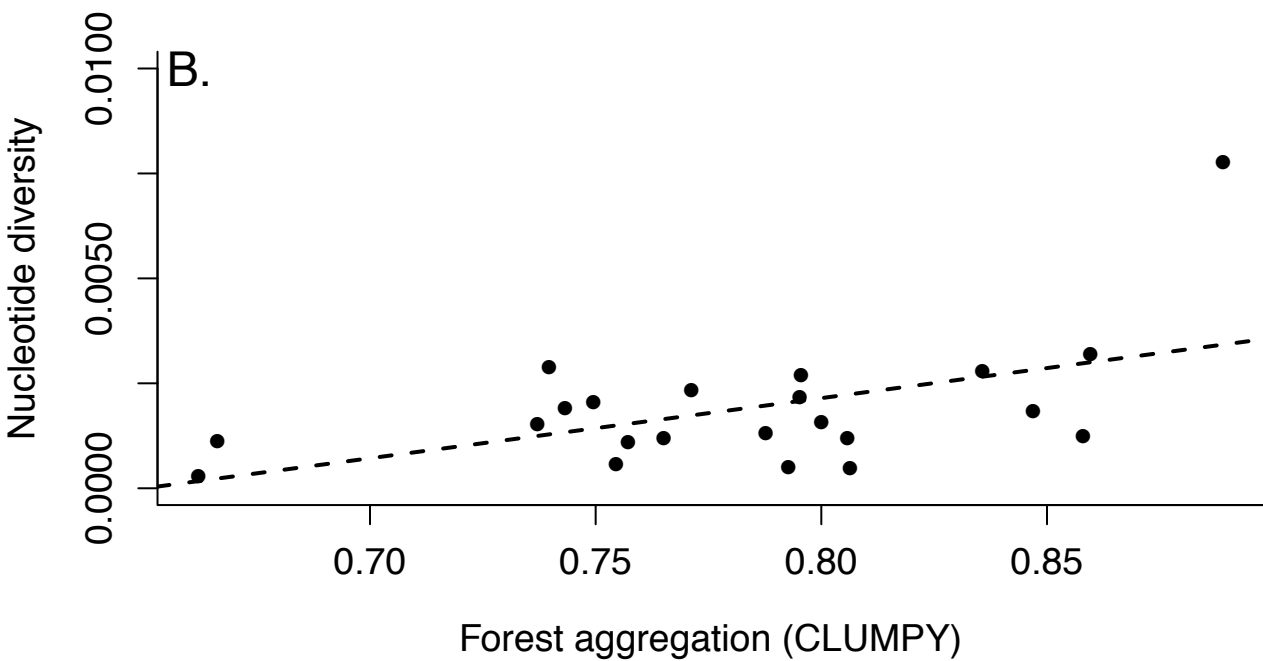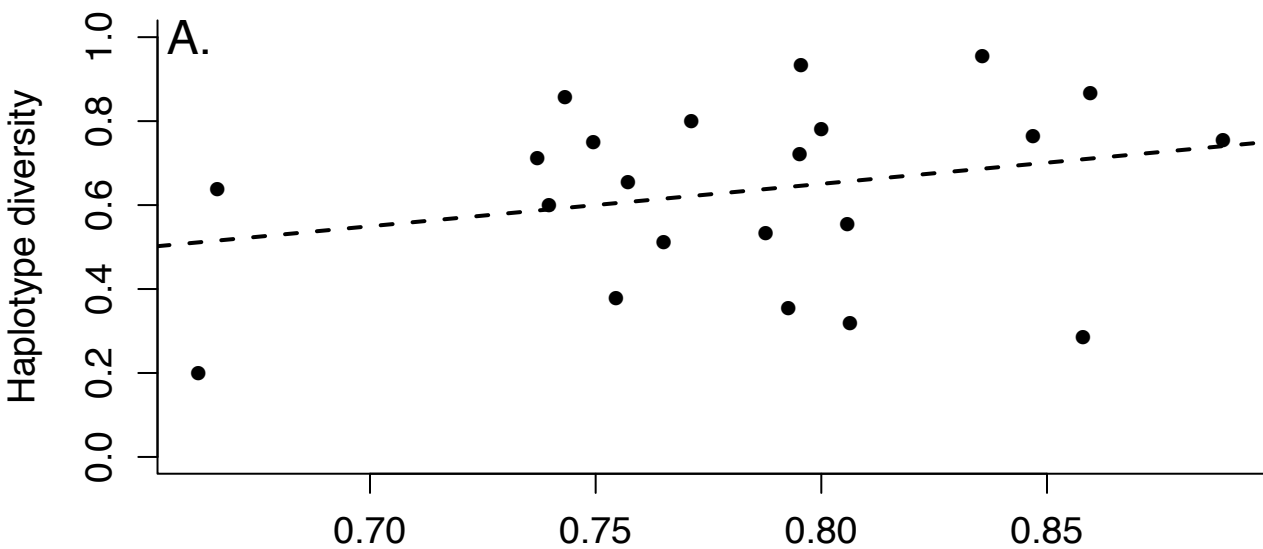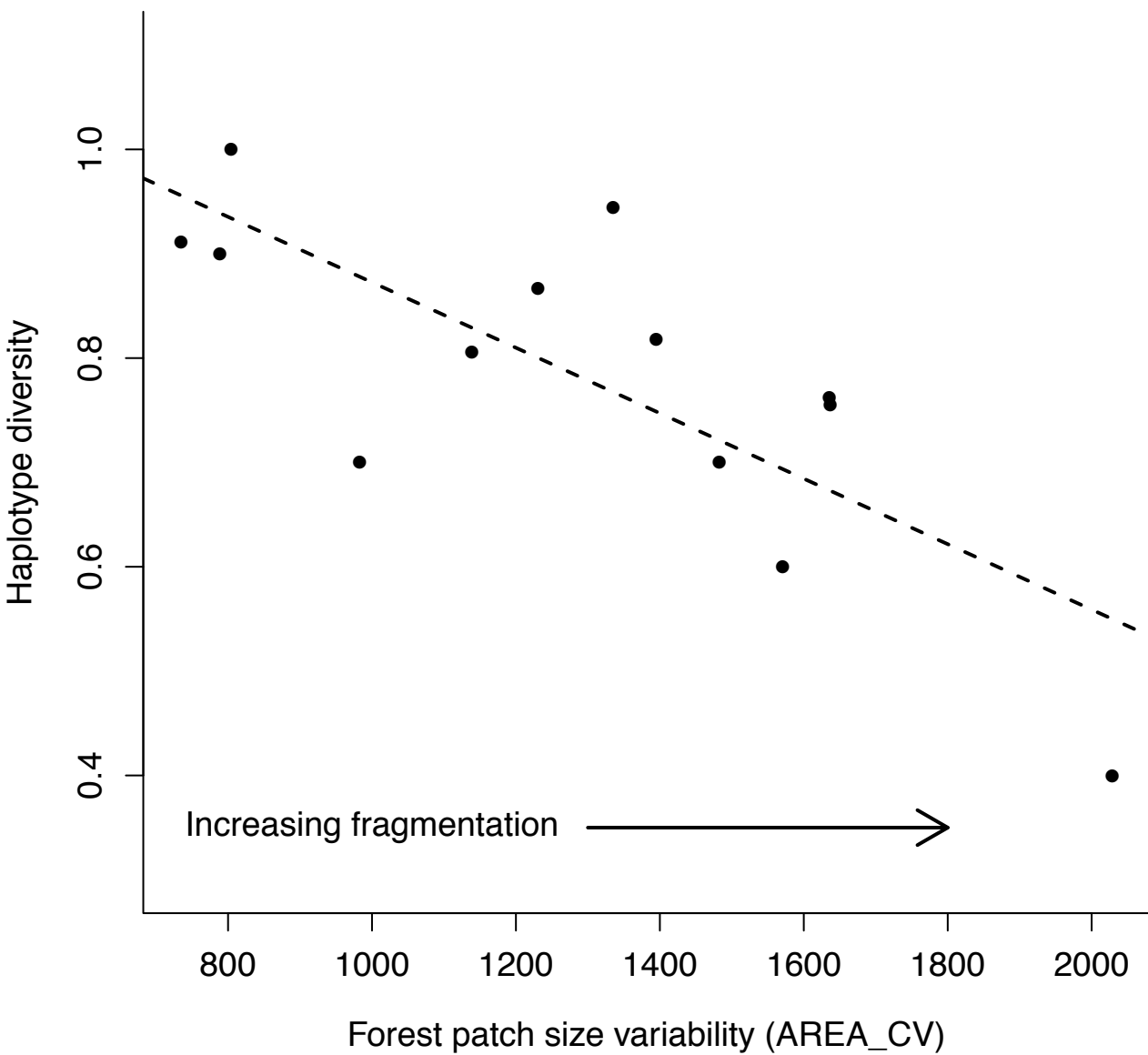
permutations within a given distance class.

584

A.

B.

Forest aggregation (CLUMPY)

A.

White−breasted Nuthatch
Mountain Chickadee
Pygmy Nuthatch

B.

White−breasted Nuthatch
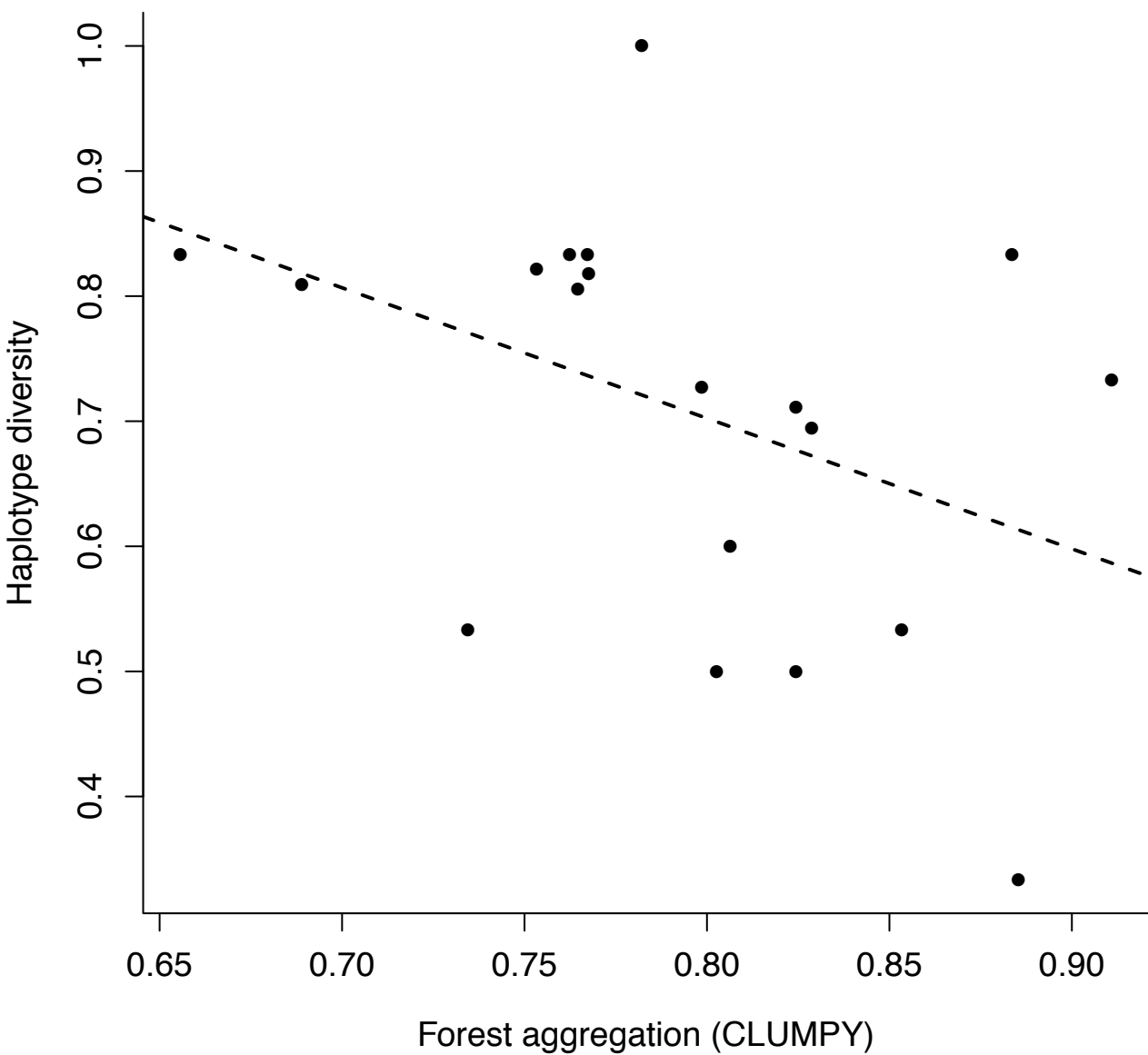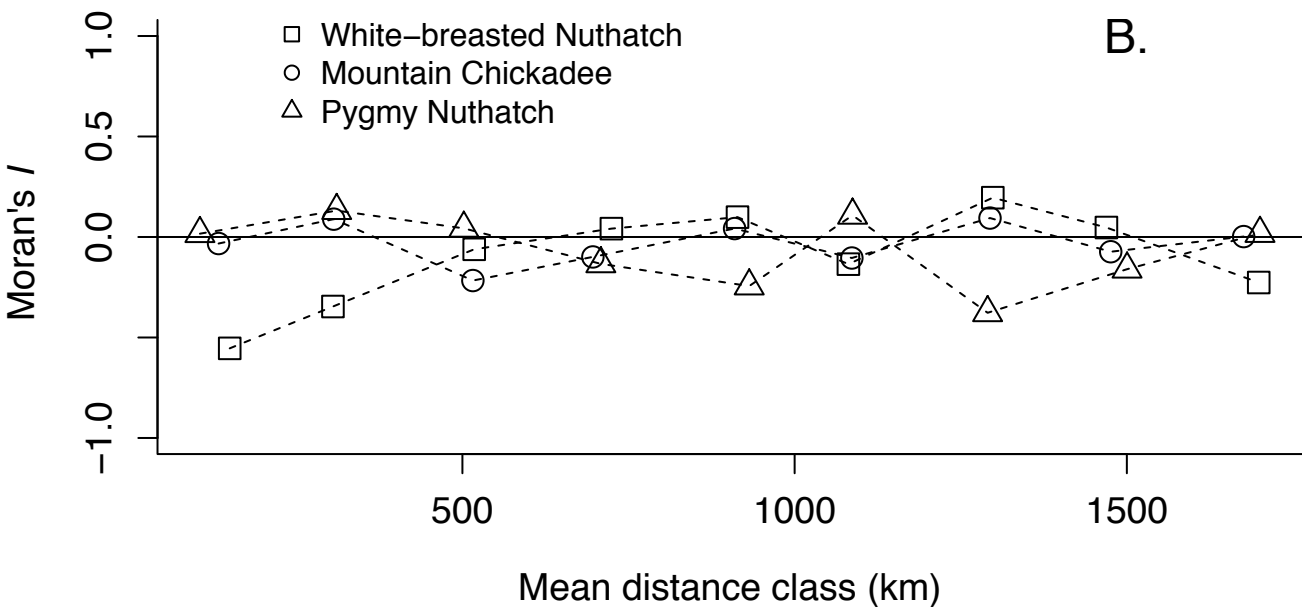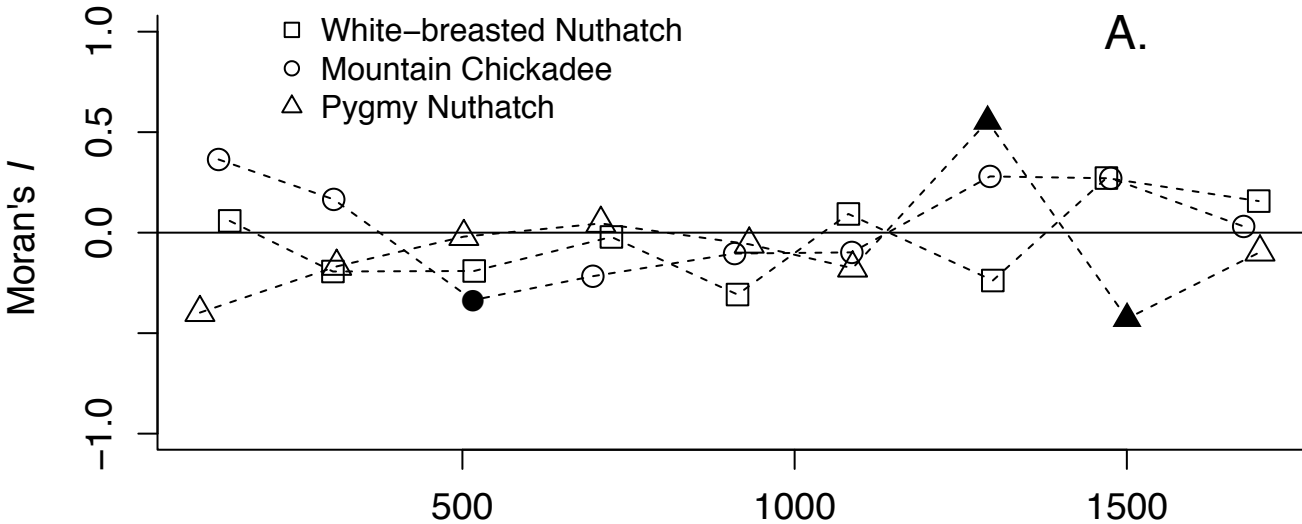Mountain Chickadee
Pygmy Nuthatch

TABLE 1. Population identifier, number of individuals sampled (n), haplotype number (number of unique haplotypes in each population), haplotype diversity and standard deviation, and pairwise nucleotide diversity and standard deviation (SD), derived from complete sequences of the mitochondrial gene NADH dehydrogenase subunit 2 (ND2), for each population from the three species used in this study.

Pop	n	Number of Haplotypes	Haplotype Diversity	Haplotype Diversity (SD)	Nucleotide Diversity	Nucleotide Diversity (SD)
				P. gambeli		
P1	8	4	0.75	0.1391	0.002058	0.001591
P2	10	3	0.60	0.1305	0.002882	0.002002
P3	10	4	0.53	0.1801	0.001313	0.001119
P4	9	3	0.64	0.1258	0.001121	0.001017
P5	10	5	0.80	0.1001	0.002337	0.001702
P6	7	2	0.29	0.1964	0.001235	0.001126
P7	10	8	0.96	0.0594	0.002786	0.001950
P8	10	7	0.87	0.1072	0.003202	0.002177
P9	10	5	0.76	0.1295	0.007781	0.004633
P10	10	7	0.93	0.0620	0.002690	0.001897
P11	10	2	0.36	0.1591	0.000512	0.000612
P12	10	3	0.51	0.1643	0.001185	0.001043
P13	10	3	0.71	0.0860	0.001537	0.001250
P14	10	2	0.20	0.1541	0.000288	0.000439
P15	10	3	0.38	0.1813	0.000576	0.000657
P16	7	4	0.86	0.1023	0.001921	0.001544
P17	11	5	0.78	0.0926	0.001572	0.001257
P18	11	5	0.76	0.1066	0.001834	0.001405
P19	12	3	0.31	0.1637	0.00048	0.000578
P20	13	4	0.65	0.1060	0.001108	0.000972
P21	9	3	0.56	0.1653	0.001201	0.001065
P22	9	5	0.72	0.1592	0.002161	0.001624
				S. carolinensis		
C1	5	2	0.60	0.1753	0.001153	0.001020
C2	5	3	0.70	0.2184	0.001537	0.001267
C3	5	2	0.40	0.2373	0.001153	0.001020
C4	11	7	0.82	0.1191	0.001537	0.001111
C5	9	7	0.94	0.0702	0.004696	0.002865
C6	5	5	1.00	0.1265	0.001921	0.001509
C7	6	4	0.87	0.1291	0.001153	0.000980
C8	7	3	0.76	0.1148	0.001006	0.000864

C9	5	3	0.70	0.2184	0.005764	0.003866
C10	5	4	0.90	0.1610	0.001921	0.001509
C11	10	5	0.76	0.1295	0.000982	0.000808
C12	9	5	0.81	0.1196	0.001067	0.000868
C13	10	7	0.91	0.0773	0.002092	0.001428
S. pygmaea						
S1	4	3	0.83	0.2224	0.001921	0.001612
S2	11	6	0.73	0.1444	0.001816	0.001264
S3	4	2	0.50	0.2652	0.000480	0.000595
S4	4	4	1.00	0.1768	0.003842	0.002888
S5	9	4	0.69	0.1470	0.001548	0.001143
S6	4	3	0.83	0.2224	0.004003	0.002993
S7	6	2	0.53	0.1721	0.001537	0.001215
S8	8	4	0.82	0.1007	0.001818	0.001316
S9	6	3	0.73	0.1552	0.003202	0.002203
S10	10	4	0.71	0.1175	0.002263	0.001521
S11	4	3	0.83	0.2224	0.003202	0.002465
S12	4	2	0.50	0.2652	0.001921	0.001612
S13	4	3	0.83	0.2224	0.002081	0.001719
S14	7	4	0.81	0.1298	0.002379	0.001668
S15	6	2	0.33	0.2152	0.001281	0.001059
S16	11	7	0.89	0.1191	0.002987	0.001892
S17	10	4	0.53	0.1801	0.001153	0.000907
S18	11	4	0.60	0.1539	0.001991	0.001359
S19	9	5	0.81	0.1196	0.002295	0.001559

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TABLE 2. Metrics used to quantify forest fragmentation within 10 km radius-landscapes. We include interpretations for only those metrics retained in the top models identified through model selection.

Metric	Description	Ecological Interpretation[a]
Forest	Percentage of landscape classified as forest in a 10-km landscape	Degree that landscape is comprised of forest
FOR	Percentage of landscape classified as forest in a 100-km landscape	Degree that surrounding region is comprised of forest
AREA_CV	Patch area coefficient of variation	Forest patch size variability, where increasing variability indicates greater fragmentation
CLUMPY	Clumpy index	Aggregation of forest patches, where positive index values indicate large, compact clusters of forest

[a]Interpretation based on Cushman et al. (2008)

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TABLE 3. Model selection results testing the relationship between fragmentation and genetic diversity for *P. gambeli*, *S. carolinensis* and *S. pygmaea*. We report Akaike's second-order information criterion (AIC$_c$), Akaike weights (w_i) and associated parameter estimates for the fragmentation metrics included in each model. Only models with strong support (ΔAIC$_c$ < 2) are presented. Forest composition at the 10 km (Forest) and 100 km (FOR) landscape scales.

	AIC$_c$	ΔAIC$_c$	w_i	n	Forest	FOR	AREA_CV	CLUMPY
P. gambeli								
Haplotype diversity								
Forest cover only	4.1	0.00	0.46		-0.13	-0.03		
Model 1	6.0	1.92	0.18		-0.12	0.01		0.06
Nucleotide Diversity								
Model 1	-217.1	0.00	0.60		0.30×10^{-3}	-0.75×10^{-3}		-0.75×10^{-3}
S. carolinensis								
Haplotype diversity								
Model 1	-4.9	0.00	0.57		-0.02	0.09	-0.12	
Model 2	-3.6	1.35	0.29	0.03	0.00	0.25	-0.11	
Nucleotide diversity								

Forest cover only	-121.5	0.00	0.78	0.23×10^{-2}	-0.26×10^{-2}		
S. pygmaea							
Haplotype diversity							
Model 1	3.8	0.00	0.25	-0.16	0.19		-0.09
Forest cover only	3.9	0.13	0.23	-0.07	0.13		
Model 2	4.1	0.33	0.21	-0.19	0.30	0.09	-0.13
Nucleotide diversity							
Forest cover only	-111.7	0.00	0.44	0.36×10^{-2}	0.74×10^{-2}		
Model 1	-109.8	1.88	0.17	0.07×10^{-2}	0.96×10^{-2}		-0.31×10^{-2}